Vol. 1 No. 2

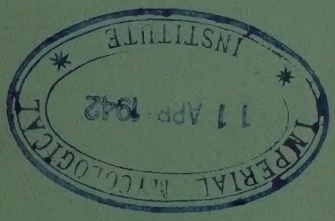
February, 1935

THE BOTANICAL REVIEW

Interpreting Botanical Progress

CONTENTS

Glacial and Postglacial Vegetation ..... Paul B. Sears 37
The Structure of the Walls of the Higher Plants
Donald B. Anderson 52



Published Monthly at
Lime and Green Sts., Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Editors and Publishers

H. A. GLEASON AND E. H. FULLING

Advisory Editors

PROF. R. W. CHANEY, paleobotany
PROF. W. S. COOPER, ecology
PROF. A. J. EAMES, anatomy
PROF. R. A. HARPER, mycology
DR. F. W. PENNELL, taxonomy
PROF. L. W. SHARP, cytology
PROF. E. W. SINNOTT, genetics
PROF. GILBERT SMITH, phycology
DR. N. E. STEVENS, pathology
PROF. R. B. THOMSON, morphology
PROF. S. F. TRELEASE, physiology

The BOTANICAL REVIEW is published monthly. Subscription rate for the United States is $3.00 per year; for Canada and other foreign countries $3.25. All subscriptions are payable in advance at par in Lancaster, Pa., or New York.

Manuscripts are prepared by contributing authors only upon invitation and on the suggestion or with the approval of the advisory editor in whose field the subject lies. Unsolicited manuscripts will not be considered. The editors, nevertheless, welcome suggestions of topics which might properly be reviewed.

All correspondence should be addressed to THE BOTANICAL REVIEW, at Lime & Green Sts., Lancaster, Pa., or The New York Botanical Garden, Bronx Park, New York, N. Y.

THE BOTANICAL REVIEW

VOL. I FEBRUARY, 1935 NO. 2

GLACIAL AND POSTGLACIAL VEGETATION*

PAUL B. SEARS

Professor of Botany, University of Oklahoma

To reconstruct the vegetation of the past involves, as does any historical research, numerous sources of error and omission. Yet reconstruction is necessary if we are to understand the changing environment of the past or to interpret modern vegetation. There is no escape from considerable, legitimate, inference based on geology as well as upon living plants and communities believed to be relicts of past conditions. But so far as possible, inference must be checked by direct evidence in the form of organic remains whose sequence and identity can be verified. In this connection pollen preserved in peat and related deposits is especially useful; and because of the close association of such deposits with glaciation they have been much employed in the study of glacial and postglacial vegetation. The results so obtained form the main basis for the following discussion which will deal first with the Pleistocene,[1] then with postglacial conditions.

On the basis of what is known of the various glacial limits and the present temperature zonation of plant life there has been considerable conjecture as to the pattern of vegetation at the times of maximum ice advance. The absence of barriers to the south and west in North America afforded a condition which does not obtain in Europe where the retreat of plants away from the ice was restricted. The general theory is that tundra, scrub, conifers and deciduous forest shifted as belts before the advancing ice, then followed back in its wake as it melted. Actually, of course, the ice

* Contribution No. 31, Bot. Lab., Univ. of Okla.

[1] The Pleistocene was the great Glacial Age during which time ice extended over 8,000,000 sq. m. of Europe and North America, and great areas of Asia and the southern hemisphere. Estimates of the duration of this period range from 500,000 years to two or three times that figure. The retreat of the ice from Sweden has been placed at 12,000 years ago and from the northern United States at least 25,000 years ago.—Editor.

lobes extended into the interior grasslands as well as into the forest regions. Moreover, the exact character of the change of climate which produced glaciation is not proved. Certainly the mere proximity of glacial ice is not enough in itself to prevent the growth of trees. Trees ferns are found within sight of the New Zealand glaciers. Spruce-fir forests develop almost at the edge of the retreating ice in Alaska and there is some evidence to show that in places the ice has advanced over standing, possibly living forests (11). In the north central states it has been difficult to find any trace of tundra plants at the base of the oldest living deposits examined, a fact which will be discussed later.

On the other hand, Piech (38) states definitely that the crest of the Riss (III) ice sheet was fronted by a strip of treeless tundra more than 100 km. wide and Firbas (19) reports similar conditions nearly 450 km. ahead of the Würm (IV) glaciation. In the Florida peat deposits Hanna finds diatoms which he considers to have been deposited during the climax of the last glaciation (27). The species are so definitely northern in character that he considers the evidence "overwhelmingly in favor of cooling." Many of the forms now occur no farther south than New England. This leads him to consider the warm Pleistocene flora found by Berry in North Carolina to be interglacial or at most intraglacial, rather than a proof that the influence of the ice did not extend far south of its limits.

The whole problem of displacement of vegetation at the maximum advance of the ice is so significant that it warrants a careful study of all of the scattered and discontinuous peat deposits south of the glacial limits. The task is enormous but it seems the best means of deciding whether glaciation was accompanied by a general and extensive lowering of temperature. Evidently snow limits were lower in tropical mountains during the Pleistocene than now and many of today's deserts were then humid. But we do not know how the latitudinal limits of the various zones beyond the ice edge were affected.

Passing from the question of glacial to that of interglacial climate, we are confronted with an embarrassing confusion as to the number, character and correlation of these interglacial stages. Opinion, even today, ranges from the belief that only one such in-

terval can be dignified by the term interglacial, all other periods of recession being intraglacial, to the belief that five or more truly interglacial intervals existed during the Pleistocene.

An excellent idea of the situation may be obtained by realizing that the Toronto interglacial beds have at different times been attributed to at least four different intervals. Of the Aftonian interval Thwaites remarks, "strangely enough, although the evidence on which the Aftonian was originally defined is worthless there is, nevertheless, a real 'Aftonian' interval of great length and possibly constituting a genuine interglacial stage" (45).

There is a growing tendency to emphasize four major glaciations during the Pleistocene. Brückner (7), with Leverett, regards them as essentially contemporaneous in Europe and North America, just as students of lesser climatic fluctuations of recent times point to a certain correlative behavior throughout the northern hemisphere. Disregarding subglaciations the scheme is as follows:

Period	*North America*	*Europe*
IV	Wisconsin	Würm
III–IV	Sangamon (Interglacial)	Riss-Würm
III	Illinoian	Riss
II–III	Yarmouth (Interglacial)	Mindel-Riss
II	Kansan	Mindel
I–II	Aftonian (Interglacial)	Gunz-Mindel
I	Nebraskan	Gunz

As to subglaciations there is still much discussion. The Iowan substage is important because of its well marked interval, the Peorian. Leverett apparently still regards these as late Illinoian, but Kay in Iowa and Leighton in Illinois have recently agreed in placing them in the early Wisconsin, thus following rather than preceding the Sangamon interglacial (8). Similarly in Europe there is some disagreement as to the position of the Warthe subglacial as indicated by Firbas and Grahmann (21) and Premick and Piech (38).

Szafer (44) in 1925 presented an account of the Polish interglacial periods in which he ascribed prolonged warm conditions, partly oceanic, partly continental to the last interglacial (Riss-Würm, Masovien II). Jessen and Milthers (32), working in Jutland and northwest Germany, agree with him, describing the last or Riss-Würm interglacial as passing up to an atlantic (warm, humid)

climax and back, with a brief temperate fluctuation during the cool closing period. The penultimate (Mindel-Riss?) is described as simpler, progressing up to a warm climax and then back to glacial conditions.

However, all of the sites except one which were described by Szafer as Riss-Würm (Masovien II) have now been correlated by Premick and Piech (38) with Mindel-Riss (Masovien I). In a detailed analysis they show the latter to have been of more marked character than the former, or last interglacial. Four beds of Mindel-Riss age show gradual progress from pine-birch through oak, then oak-linden-hornbeam to fir, fir-spruce, and back to pine. During this final pine stage there appears to have been a brief amelioration marked by temporary increase in oak and other hardwoods. These quickly vanished before pine, arctic birch and willow, heralds of the returning ice. A similar analysis of the last interglacial agrees in its general import but differs in detail, presenting a predominantly cool and moderately humid character. It appears to have been mainly coniferous with briefer and weaker expressions of the mixed oak phase.

Dokturowsky (14) has found similar conditions for the last interglacial in Russia. Following the Riss-ice was a cold period with pine, birch and willow. This was succeeded by a warm period with hazel, alder and mixed oak forest, while another cold period with spruce and fir preceded the Würm glaciation. Dokturowsky is unable to confirm Szafer's report of a prolonged and intricate character for the last interglacial. With respect to the preceding, interglacial information from Russia is scanty, remains of yew, beech, larch and Trapa appearing to comprise the finds reported. Brookes, with others, considers the penultimate or Mindel-Riss as of much greater length and more marked character than the other interglacial periods, and states that it should probably be correlated with the prolonged Yarmouth stage in North America.

Firbas and Grahmann (21) report that deposits following the Warthe subglaciation in south Brandenberg show fluctuation between birch and pine, the latter accompanied by traces of deciduous forest. The period appears to have been predominantly cool. Spruce appears, although afterwards completely absent from the late glacial and early postglacial stages in the same vicinity.

In addition to these more comprehensive recent studies there is a considerable number having to do with isolated and fragmentary profiles, correlated with varying degrees of certainty. From all of the work to date, incomplete as it is, certain principles appear clearly enough. There is a general and significant, even if not detailed, parallel between the events of postglacial time and those of the interglacial intervals, so far as the latter are known. In the second place there was a sufficient variety of mild climates during one or more of the intervals to have permitted extensive migrations of plants, including some which had been thought of as tertiary rather than as interpleistocene relicts (44).

For North America, the contents of the Toronto beds show that during whatever interglacial period they were laid down, vegetation flourished, which suggests a milder climate than that of Toronto today (10). Toronto is within but near the present northern range limit of the linden and papaw, while the natural range of the Osage orange is distinctly restricted to the southwestern Mississippi Valley.

Evidence of a marked interglacial climate during what Kay considers the Aftonian, or first interval, has been secured by Lane working with the Iowa Geological Survey. His results have not yet been published but the writer has examined, and in some cases checked, his material. Acknowledgment is here made for courteous permission to refer to this and other data in advance of publication. Lane finds evidence in the Denison beds of a prolonged steppe or grassland period which passes through a brief deciduous forest phase into coniferous forest.

Two independent studies have been made on the Sangamon, an unpublished one by Lane on the Wapello beds in Iowa, the other by Voss (47) in Illinois. The results of both studies are in substantial agreement. Voss reports vegetation indicating conditions in Illinois similar to those of the conifer belt of the northern states and southern Canada. Lane finds conifers throughout. Pine with grass, oak and spruce later yields to a cover of pine and spruce. The Wapello beds are considered late Sangamon.

The Peorian, now considered intraglacial, whether within the late Illinoian or early Wisconsin, has also been studied by Voss, with findings of a conifer climate similar to that described by him for the Sangamon. The climatic resemblance of the Sangamon to

the Peorian is much more consistent with the recent reports from Poland regarding the Riss-Würm than with the earlier report of Szafer or the findings of Jessen and Milthers in Jutland and northwest Germany.

In addition to the report of Voss on the Peorian, we have reports on intraglacial beds of late Wisconsin age from Wilson (49) in Manitowoc County, Wis., and from Cooper and Foote (12) in Minneapolis. Both agree that the organisms found indicate conditions now prevalent to the north of the sites investigated, thus confirming their intraglacial character.

Before leaving the subject of climate during the glacial period, it seems advisable to mention the importance of the loess. This wind deposited soil is considered an excellent criterion of dry conditions. Several occurrences of it have been correlated as interglacial and so used to predicate marked continental conditions during those intervals. This assumption is strengthened, not only from the character and mode of origin of the loess itself, but from the character of the molluscan remains which it shows. Baker (4) has studied the latter in loess deposits of the Yarmouth, Sangamon, Peorian and two Wisconsin intraglacial periods. In addition to several extinct species he finds others whose present range is definitely western or northern. If practicable it would be of interest to see the same statistical methods applied to molluscan remains which have proved so useful in the case of fossil pollen.

Five distinct soil horizons, separated by loess, have been described from Bermuda by Sayles (40). The soils have been attributed to mild humid inter-glacial conditions, while the loess is considered to be due to the severe, windy periods of glacial advance. Harper (28) has found somewhat similar conditions in Oklahoma which he ascribes to the Pleistocene. The Rocky Mountain region and the Southwest abound in fossil soils or humified layers separated by layers of aeolian material or heavy alluvial wash suggesting arid intervals, but their correlation is necessarily a difficult matter, requiring great caution.

The climate and vegetation of postglacial times has been much more thoroughly studied than have Pleistocene conditions. Nearly 100 years ago in the Danish peat bogs, Steenstrup found successive strata of buried forests not showing evidence of a steadily warming climate since glacial times. As decades went by, the study of

fossil remains in the peat and of the peat layers themselves suggested strongly that the climate of Europe had once been milder than today. This probability seemed to be increased by the presence of relict steppe plants in places having today a forest climate.

The solution of the problem was greatly complicated by historical, traditional and even stratigraphic evidence indicating climate fluctuations of considerable intensity but short duration. Moreover, the destruction of plant cover and humus following human occupation always tends to create an impression of greater aridity than the climate justified, except perhaps in areas having a marked oceanic climate. This, of course, confuses the issue and has doubtless been responsible for much of the prevalent notion that our present climate is becoming drier. That it is becoming cooler seems warranted by the cultural history of Iceland, the Esquimaux, and by the southward shift of the limits of the vine.

Hypothesis has passed through four important phases as follows:

First, the simple assumption that vegetation had moved south before the advancing ice and subsequently returned to a more or less stable equilibrium. This idea is still implicit in many quarters (24, 48).

Second, the Blytt-Sernander hypothesis, postulating a series of fluctuations in both moisture and temperature, and designating the following periods: pre-boreal, boreal, atlantic, sub-boreal, sub-atlantic. The atlantic or middle period was conceived of as a climatic optimum, warm and humid, between the very continental boreal and sub-boreal. The sub-atlantic represented a return of humidity. The stages so set forth were associated with a definite stratigraphy and archeology, and dated with great accuracy through the method of DeGeer (42). They thus afforded something very tangible, capable of being checked with most minute care throughout Europe. The value of this hypothesis as a scientific tool is not to be underestimated, even by those who have rejected it. As is often the case, it has probably suffered more from its friends than its enemies.

Third, G. Anderson (1), holding the view that temperature changes have been the predominant ones, conceded that glaciation was followed by a very dry and ultimately warm boreal period, succeeded in turn by an equally warm but much wetter atlantic. But he denied the reality of a second dry or sub-boreal period and

predicated a gradual climatic deterioration from the atlantic (neolithic) down to the present. In this general interpretation Gross (25) and Rudolph (39) appear to concur.

Fourth, L. von Post (46) divides postglacial time into three periods: 1., a period of increasing warmth; 2., a period of maximum temperature; 3., a period of decreasing temperature. On this general frame-work, he admits, lesser fluctuations of the various climatic factors have had their place. Under suitable conditions the minor fluctuations have doubtless been extreme enough to produce a marked effect. Very soundly, he concludes that only by the most minute analysis between correlated horizons, on a widely coordinated plan, can we determine the extent, character and intensity of the actual fluctuations. Gams (22) appears to agree essentially with von Post but considers that the waning of the warm continental maximum has occurred in oscillating fashion, thus explaining whatever evidence may exist for a dry sub-boreal about 3000 years ago. He also considers the evidence of recent drying not to be wholly due to human interference.

Having thus outlined the trends of theory, let us examine the phenomenology upon which they are based. The difficulty of accepting an hypothesis of return to stable climatic equilibrium following glaciation in Scandinavia has already been noted. The pioneer work of Steenstrup was followed by much more detailed study of bog profiles, plant fossils and molluscan remains, much of which went counter to the idea of a stable postglacial equilibrium. Both in Europe and North America taxonomists and students of floristics found themselves confronted with problems to be explained only by assuming a warm continental climax some time during the postglacial (23). Geological analysis of glacial retreat showed that it had been marked by periods of re-advance. Furthermore, the demonstration of huge-scale fluctuations, such as the Permian[2] and Pleistocene as well as the so-called "cycles" of small magnitude have, it must be confessed, placed scientists in a receptive mood toward the demonstration of fluctuations of an intermediate order, to be measured in tens of centuries perhaps.

[2] Permian time antedated the Pleistocene by great eons. It succeeded the Carboniferous as the last of the Paleozoic. In South Africa, India and Australia evidences of glaciation during this earlier epoch, too, have been found. During Permian time conifers probably made their first appearance on earth. —Editor.

Allowing for appropriate differences in alpine and other extreme habitats, the general vegetational history in Europe has been about as follows. Widespread and prolonged postglacial tundra conditions are indicated by remains of *Dryas,* birch and willow, far south of the ice front. It is generally found that this was succeeded by a period in which pine predominated, variously accompanied by birch and hazel. The pine was followed by oak, the hazel frequently persisting on into the oak period. In fact, hazel, considered to be an indicator of dry continental conditions, exhibits a singular behavior so far as its relative pollen frequency is concerned. Its maximum may precede, accompany or follow that of the oak. Perhaps as much as any other factor this contributes to the uncertainty as to whether conditions were dry during both the pine (boreal) and oak (sub-boreal) or only during the former. Erdtman (15), in a very penetrating analysis, points out certain contingencies which may affect preservation of the hazel pollen even when abundant, while Firbas (20) notes that weathering of peat during the hazel maximum may interfere with the study of its pollen content. In the words of Theophrastus, "this, then, is proper subject for further investigation."

The oak period, characterized by an admixture of other deciduous trees such as linden and elm, exhibits a variable length and intensity of expression. It is least marked at high altitudes and latitudes, more so in continental than oceanic areas. In a large part of Europe the oak appears to have been replaced eventually, either through an intermediate stage of beech or without it, by conifers, birch and alder, suggesting cooler and perhaps more humid conditions.

In addition to the changes of vegetation, as shown by pollen analysis, the changing character of the peat itself affords some evidence. In the late glacial stages peat formation seems to have been restricted and exceedingly slow which has prevented an adequate record of events and measure of time. With the establishment of a sub-arctic forest of birch and pine, heavy formation of sedge peat occurred. Later during the warm, dry (boreal) climax (hazel) this peat was subjected to heavy humification which often spoiled the record. During the mixed oak stage, formation was renewed (atlantic) but apparently often this was followed by another period of weathering (sub-boreal). On the latter point there is consid-

erable controversy between those who believe in a dry sub-boreal, and their opponents. The weathered sub-boreal (?) layer in question is known as the Grenz-horizont. According to Gross (26) its origin and even existence is frequently a matter of doubt. Above the mixed oak strata is found a renewal of peat formation, rather generally attributed to "climatic deterioration"—either lowered temperature, increased moisture or both. Quite generally the surface layers of peat show disturbance, attributed by many to cultural effect, but thought by others to be due to a recurrence of dryness.

There is apparent a growing and hopeful effort to isolate all of the factors such as migration rate of trees, late glacial interstages, local plant succession, soil development and climatic change. The reader interested in further information should consult the recent, more general papers of Gams (22), Gross (25), Firbas (19), Keller (34), von Post (46), Rudolph (39) and others cited by Erdtman (17).

By comparison with Europe, North American studies are still meagre and tentative. The area is vast and diversified with its own geological history. The absence of marked barriers to plant migration and a decidedly richer forest flora than that of Europe introduce complications. Although there is a growing belief in the similarity of climatic trends, it is essential that the American problem be approached from a strictly objective basis.

As in Europe, the known peat record does not extend back continuously beyond a maximum of about 10,000 years. Such late-glacial records as are known appear to be isolated and to indicate general northerly conditions, one from the Connecticut valley being pronounced by Hollick (29) to be the American equivalent of the European Dryas flora. There is not much but conjecture as to conditions beyond the ice-front, although Hanna's (27) report of diatoms in northern Florida which now range from New England northward is significant.

There appears to be little or no record of tundra at the bottom of living peat profiles. Instead, the record begins with a marked abundance of fir and spruce pollen, not only in southeastern Canada (3) and the Lake States (41) but even in Iowa (35). This does not preclude the possibility of a long tundra stage. The basins suitable to peat formation may have been occupied by dead ice until the forest returned northward to surround them. Tundra

may possibly have been followed by steppe conditions so dry as to preclude peat formation. Or, as in Alberta (16), the central states may have been covered with an aspen parkland and yet have shown a pollen profile in which only conifers were indicated. Antevs (2), in common with many others, believes that a tundra zone existed but that it may have been comparatively narrow. Further study may elucidate this point.

While the bottom of the record in eastern North America shows the general presence of spruce and fir, above that point important regional differences appear. In southeastern Canada (3), Minnesota and Northern Wisconsin (48) pine quickly replaces the other two coniferous genera and is predominant until the upper layers where spruce and fir once more increase at the expense of pine. Whatever indications of deciduous trees there may be, they are strongest during the middle of the pine period, not inconsistent with the idea of warmer conditions than now obtain. In Canada, hemlock shows a slight but definite tendency to appear before and after the pine, rather than with it. This suggests to Auer that the pine corresponds to the European sub-boreal, preceded and followed by more humid periods, the atlantic and sub-atlantic, respectively. On the other hand, Voss reads no such meaning into his own profiles from the north lake states although he concedes their similarity to those of Auer. He attributes the recent increase of spruce to local conditions without discussing their striking coincidence with local effects across half of this continent, not to mention northern Europe and Japan (33).

Profiles from central Wisconsin (48) and in less detail from Michigan (37) and northern Indiana (31, 36) resemble in their general character those just described save that there is a definite interval of deciduous predominance instead of a mere showing during the pine period. To varying degrees these profiles show indications of a recent increase of conifers at the expense of deciduous genera, again suggesting the passing of warmer conditions.

In Ohio (41), central Indiana (31) and northern Illinois (48), following the conifers, the deciduous interval is marked and prolonged through to the present. In northern Illinois, where it occupies the upper two thirds of the profile, Voss states that climate has been essentially uniform and attributes any fluctuations to edaphic and topographic causes. In Ohio the fir and spruce are first re-

placed by pine. The deciduous forest interval then begins with an appearance of white pine, beech and hemlock, later showing a predominance of oak-hickory with a recent and slight but definite increase in beech. Sears has interpreted the oak-hickory period as dryer, perhaps warmer than those which preceded and followed it. The transition from coniferous to deciduous he considers to be moister than the pine period which preceded it.

In Iowa (35) the coniferous stage passed through one of deciduous forest into grassland near the base of the profile. The grassland shows at least two periods of abundance of pollen, indicating semi-arid conditions. Sears has correlated these tentatively with the pine and oak-hickory periods in Ohio, and the latter with Auer's pine period in Canada.

It must be conceded that any correlations at the present time are highly provisional and that an immense amount of work needs to be done. The first task is to establish the broad outlines of major change. A simple approach should be to test whether von Post's hypothesis of increasing warmth, warm maximum, and decreasing warmth is justified as it seems to be by much of the work except that in Illinois. In a transitional region like Illinois it is essential that search be made for strata showing grass pollen and that species, as well as genera, having a complementary character be studied. In Ohio this was done by using beech and hickory. Hotchkiss and Ingersoll (30) report geothermal measurements from the Calumet district which agree with the requirements of von Post's outline. Incidentally, Dachnowski (13) reports petrographic sequences in his peat profiles such as would be expected if not only the general hypothesis of von Post but the moisture fluctuations postulated by Auer and Sears were a reality. Certainly these assumptions all need much more rigorous proof than they have at present. Complications may be expected because of human disturbance of recent vegetation and the possibility, however remote, that there has also been a recent swing towards drier climatic conditions. Furthermore, it is essential to reckon with the probability that climatic shifts, if any, "have not operated uniformly nor persisted equally in all types of habitat" (42).

In the meantime, there is a healthy enough divergence of viewpoint among American students to insure that any hypothesis whatsoever will be thoroughly tested, including the hypothesis that

much of postglacial climate has been uniform (3, 6, 9, 13, 24, 42, 48).

References

1. Andersson, G. Die Veränderungen des Klimas seit dem Maximum der letzten Eiszeit. Cong. Geol. Internat. 11th Session **1**: 371–377. 1910.
2. Antevs, E. The Quaternary ice age in North America. Brooklyn Bot. Gard. Rec. **21**: 186–202. 1932.
3. Auer, V. Peat bogs in southeastern Canada. Can. Geol. Surv. Mem. **162**: 1–32. 1930.
4. Baker, F. C. Molluscan life of the loess deposits of Illinois. Trans. Ill. St. Acad. Sci. **20**: 269–292. 1928.
5. Barkley, F. A. The statistical theory of pollen analysis. Ecology **15**: 283–289. 1934.
6. Bowman, P. W. Study of a peat bog near the Matamek River, Quebec, Canada, by the method of pollen analysis. Ecology **12**: 694–708. 1931.
7. Brückner, E. Über die Klimaschwankungen der Quartärzeit und ihre Uhrsachen. Congr. Geol. Internat. 11th Session **1**: 379–389. 1910.
8. Bryan, K., et al. Reviews of papers on the geomorphology of North America, 1932/33. Zeitschr. Geomorphologie **7**: 1–42. 1932/33.
9. Cocke, E. C., Lewis, I. F., and Patrick, R. A further study of Dismal Swamp peat. Am. Journ. Bot. **21**: 374–395. 1934.
10. Coleman, A. P. Ice ages recent and ancient. 1–296. New York, 1929.
11. Cooper, W. S. A third expedition to Glacier Bay, Alaska. Ecology **12**: 61–95. 1931.
12. Cooper, W. S., and Foot, H. Reconstruction of a late-Pleistocene biotic community in Minneapolis, Minn. Ecology. **13**: 63–72. 1932.
13. Dachnowski-Stokes, A. Records of climatic cycles in peat deposits. Rep. 2nd. Conf. on Cycles. 55–64. Washington, 1929.
14. Dokturowsky, W. S. Die interglaziale Flora in Russland. Geol. Fören. Förhandl. **51**: 389–410. 1929.
15. Erdtman, G. Boreal forests and the theory of pollen statistics. Journ. Ecol. **19**: 158–163. 1931.
16. ————. Worpswede-Wabamun. Abh. Nat. Ver. Bremen. **28**: 11–17. 1931.
17. ————. Literature on pollen-statistics and related topics published in 1932 and 1933. Geol. Fören. Förhandl. **56**: 463–481. 1934.
18. ————, and Erdtman, H. The improvement of pollen-analysis technique. Svensk Bot. Tidskr. **27**: 347–357. 1933.
19. Firbas, F. Die Vegetationsentwicklung des mitteleuropäischen Spätglazials. Nachr. Ges. Wiss. Göttingen VI. NF **1**: 17–24. 1934.
20. ————. Zur spät- und nacheiszeitlichen Vegetationsgeschichte der Rheinpfalz. Beih. Bot. Centr. **52**: 119–156. 1934.

21 ————, AND GRAHMANN, R. Über jungdiluviale und alluviale Torflager in der Grube Marga bei Senftenberg (Niederlausitz). Abh. Math.-Phys. Kl. Sächs. Akad. Wiss. **40**: 1–63. 1928.
22. GAMS, H. Die vegetations- und klimageschichtliche Bedeutung der Alpenseen und Alpenmoore. Forsch. u. Fortschr. **8**: 197. 1932.
23. GLEASON, H. A. The vegetational history of the Middle West. Ann. Assoc. Am. Geog. **12**: 39–85. 1923.
24. GRIGGS, R. F. The edge of the forest in Alaska and the reasons for its position. Ecology **15**: 80–96. 1934.
25. GROSS, H. Das Problem der nacheiszeitlichen Klima- und Florenentwicklung in Nord- und Mitteleuropa. Beih. Bot. Centr. Abt. II, **47**: 1–110. 1931.
26. ————. Zur Frage des weberschen Grenzhorizontes in den östlichen Gebieten der ombrogenen Moorregion. Beih. Bot. Centr. **51**: 305–353. 1933.
27. HANNA, G. D. Diatoms of the Florida peat deposits. Ann. Rep. Fla. State Geol. Surv. **23–24**: 65–96. 1933.
28. HARPER, H. J. Further investigations of buried soils in relation to climatic changes in Oklahoma. Proc. Okla. Acad. Sci. **14**: 65–67. 1934.
29. HOLLICK, A. Plant remains from a pleistocene lake deposit in the upper Connecticut River valley. Brittonia **1**: 35–55. 1931.
30. HOTCHKISS, W. O., AND INGERSOLL, L. R. Postglacial time calculations from recent geothermal measurements in the Calumet copper mines. Jour. Geol. **42**: 113–122. 1934.
31. HOUDEK, P. K. Pollen statistics from two Indiana bogs. Proc. Ind. Acad. Sci. **42**: 3–7. 1933.
32. JESSEN, K., AND MILTHERS, V. Stratigraphical and paleontological studies of interglacial freshwater deposits in Jutland and northwest Germany. Danm. geol. Unders. II, **48**: 1–379. 1928.
33. JIMBO, T. Pollen analytical studies of peat formed on volcanic ash. Sci. Rep. Tôhoku Imp. Univ. ser. 4. **7**: 129–132. 1932.
34. KELLER, P. Wandlungen des Landschaftbildes in prähistorischer Zeit. Arb. Prähist. Abt. hist. Mus. St. Gallen **1**: 1–57. 1933.
35. LANE, G. H. A preliminary pollen analysis of the East McCulloch peat bed. Ohio Journ. Sci. **31**: 165–171. 1931.
36. LINDSEY, A. J. Preliminary fossil pollen analysis of the Merrillville white pine bog. Butler Univ. Bot. Stud. **2**: 179–182. 1932.
37. POTZGER, J. E. Succession of forests as indicated by fossil pollen from a northern Michigan bog. Science **75**: 366. 1932.
38. PREMIK, J., AND PIECH, K. Zur Kenntnis des Diluviums im süd-westlichen Mittelpolen. Ann. de la Soc. Géol. de Pologne **8**: 1–132. 1932.
39. RUDOLPH, K. Grundzüge der nacheiszeitlichen Waldgeschichte Mitteleuropas. Beih. bot. Centr. **47**: 111–176. 1930.
40. SAYLES, R. W. Bermuda during the Ice Age. Proc. Am. Acad. Arts and Sci. **66**: 379–467. 1931.

41. Sears, P. B. Postglacial climate in eastern North America. Ecology **13**: 1–6. 1932.
42. ————. Climatic change as a factor in forest succession. Journ. For. **31**: 934–942. 1933.
43. Sernander, R. The warm postglacial period and the postglacial climatic deterioration of northern Europe. Proc. Int. Congr. Plant Sci. Ithaca **1**: 663–666. 1926.
44. Szafer, W. The climatic character of the last interglacial period in Europe. Proc. Int. Congr. Plant Sci. Ithaca **1**: 647–653. 1926.
45. Thwaites, F. T. Outline of glacial geology. 1–115. Ann Arbor, 1934.
46. von Post, L. Problems and working-lines in the postarctic forest history of Europe. Proc. 5th Int. Bot. Congr. Cambridge. 48–54. 1930.
47. Voss, J. Pleistocene forests of central Illinois. Bot. Gaz. **94**: 808–814. 1933.
48. ————. Postglacial migration of forests in Illinois, Wisconsin and Minnesota. Bot. Gaz. **96**: 3–43. 1934.
49. Wilson, L. R. The Two Creeks forest bed, Manitowoc County, Wisconsin. Trans. Wisc. Acad. Sci. **27**: 31–46. 1932.

THE STRUCTURE OF THE WALLS OF THE HIGHER PLANTS

DONALD B. ANDERSON
Associate Professor of Botany, University of North Carolina

The presence of a definite more or less rigid wall enclosing the protoplasm is one of the important characteristics of plant cells, but the structure and chemical composition of this wall varies enormously when the entire plant kingdom is considered. The origin of these conspicuous cellular membranes, the details of their structure and the changes that they undergo during the growth of the organism have interested botanists for nearly a century. It is interesting to note, however, that the structure of the plant cell-wall can no longer be regarded as a problem of strictly botanical interest. The wide use of cellulose in modern industry has focussed the attention of workers in many different fields upon the problems of cell-wall structure. Papers dealing with these problems may be found about as frequently in the professional journals of the chemist and physicist as in those of the botanist. The development of new methods of investigation has made it possible to discover structural units in the wall that are far beyond the range of the finest modern microscopes. Not only can the existence of these submicroscopic units be detected but their spatial arrangement in the wall can be determined with some precision and the changes that they undergo during the development of the wall can be studied. Dependable information regarding the molecular orientation of substances composing the structures of the cell-wall has seemed, until recently, far beyond the limits of human ingenuity. It is now, however, definitely within the scope of experimental study and entirely possible for the botanist to obtain very concrete pictures of the spatial arrangement of the molecular groups that make up the cell-wall as well as of the orientation of the various atoms that make up these molecular groups. Before undertaking a discussion of these recent developments it will be desirable to sketch briefly the evolution of ideas regarding plant cell-wall structure.

The prominence of the plant cell-wall led to the discovery of the cellular structure of plants. It was only natural that early observers should have been impressed with the cell-wall and formed

exaggerated ideas regarding its rôle in vital activity. The discovery of protoplasm and the gradual realization of its fundamental significance transferred interest from the conspicuous cell-wall to the contents of the cell. The wall lost its position of preëminence in the minds of investigators and became generally considered as a passive non-living membrane surrounding the active protoplasm. This idea of the wall as being sharply and distinctly separated from the living protoplasm, as being a dead non-living material produced by protoplasmic activity, has persisted until very recent time.

The wall of the plant cell is not homogeneous but shows definite lamellae when viewed in cross-section. These lamellae usually differ in their refractive indices and, consequently, appear with different degrees of brightness. In addition to this stratification within the wall, surface markings of various kinds, especially spiral striations, are frequently visible. These structural features of the wall become more conspicuous when the wall is swollen with suitable reagents and they decrease in visibility as the wall is dehydrated. When cross-sections of cell-walls are viewed between crossed-Nicols[1] certain lamellae in the wall appear dark, i.e., isotropic, while other lamellae show varying degrees of double refraction.

These facts led Nägeli (39), who made the first extensive study of cell-wall structure, to suggest that the wall was composed of submicroscopic units or *micellae* arranged in definite layers. Each micelle was believed to be surrounded by a layer of water and so separated somewhat from adjacent micelles. The stratification visible in cross-section was explained by assuming a difference in the size of the micelles and, therefore, a difference in the amount of the adsorbed water. Stratification was, accordingly, believed to be the result of micellar layers of material with relatively large amounts of adsorbed water alternating with layers of micelles with smaller amounts of adsorbed water. Differences in the amount of swelling along different cell axes were explained by assuming the micelles to be elongated. Cubical micelles would have equal amounts of adsorbed water on all sides while elongated micelles would form a membrane having more adsorbed water in one axis than in another. This micellar theory of Nägeli has been the ob-

[1] For definition of crossed-Nicols see Gage, S. H., The Microscope.—Editor.

ject of considerable discussion and debate for nearly three quarters of a century. The most modern methods of cell-wall investigation have only served to emphasize its essential accuracy and today it is probably more widely accepted than any other theory of cell-wall structure.

Early investigators discovered the fact that various lamellae in the wall reacted differently to dyes. Certain lamellae stained intensely with specific dyes while others stained only slightly or not at all. This phenomenon was rightly interpreted to indicate the presence of chemically different materials in the wall. The existence of chemically different materials in the wall was also shown by the action of various solvents.

The most important constituent of the wall is cellulose since it forms the skeletal framework of most plant cell-walls. Associated with cellulose in the cell-wall are five other common membrane substances: *lignin,* an amorphous material, generally associated with cellulose in woody tissue; *pectic compounds,* substances of colloidal character that make up the original middle lamella and occur with cellulose in most plant cell-walls; *hemicelluloses,* wall compounds that are polymers of pentose and hexose sugars and that can be hydrolyzed with hot dilute acids; *cutin* and *suberin,* compounds with lipoid properties that occur in epidermal cell-walls, cork tissue and in a few highly specialized cell-walls. In addition to these membrane materials the cell-wall may contain greater or lesser amounts of minerals and organic compounds that play no essential part in its structure.

The Origin of the Cell-Wall

The exact mechanism by which the cell-wall originates in the higher plants is not definitely known. The new cell-wall is usually formed after nuclear division. A protoplasmic plate, the *cell-plate,* forms between the daughter nuclei. Early investigations led to the belief that the cell-plate was formed from the spindle fibers but the investigations of Bailey (4) and others (46) indicate that the cell-plate may continue to develop after nuclear division is complete. Two views of the formation of the first wall are current: (a) the cell-plate divides longitudinally and the new wall is deposited in the cleft between the two halves of the cell-plate; (b) the cell-plate itself becomes transformed into the material of the

wall either through a change in its composition or as a result of the addition of new material. It seems possible, in the light of recent work as discussed by Sharp (46), that the cell-plate of the earlier workers is an artifact produced by the fixing agents used. Recent work (46) indicates that the region between the daughter nuclei is actually more liquid than the adjacent protoplasm and that membrane materials are deposited in this liquid zone forming the first wall between the daughter nuclei. There is abundant evidence that the cell-plate develops independently of the spindle fibers between the daughter nuclei and that a large proportion of this first wall is formed by the growth and extension of the terminal portions of the cell-plate itself.

However the first wall between the cells may be formed it is known to be composed of pectic material. To this pectic material between the protoplasts of the adjacent cells, a layer of cellulose containing pectic material is subsequently added by each protoplast. This first cellulose layer forms the primary wall. It differs in several essentials from subsequent layers of cellulose that may be added to this membrane during the thickening of the wall. The primary wall is capable of growth and enlargement and of undergoing reversible changes in thickness (29). The secondary wall consists of all the subsequent cell-wall material deposited within the primary wall. This material is usually added in the form of definite lamellae which, as a rule, are not identical in their physical and chemical properties. Because of these differences in chemical or physical properties the secondary wall itself is sometimes subdivided. This interpretation seems unwise in view of the fact that the secondary walls of different cells differ greatly in their structure and additional subdivisions of the cell-wall into tertiary or quarternary deposits could have no general application or any uniform morphological significance.

The terms *middle lamella, primary wall* and *secondary wall* have not been used by different investigators to apply to the same structural portions of the cell-wall. This has led to considerable confusion and it is necessary for each worker to define his use of the terms. In an effort to clarify this situation and to bring some order out of the present confusion of cell-wall terminology, Kerr and Bailey (29) have carefully reinvestigated the subject and proposed the following use of terms:

1. *Middle lamella* or *Intercellular material* as the amorphous, isotropic[2] material largely, if not entirely, pectic compounds first deposited by the cytoplasm.

2. *Primary wall* or *cambial wall* as the first anisotropic[2] layer of the wall composed largely of cellulose and pectic materials. It is capable of growth and extension and has the capacity for undergoing reversible changes in thickness.

3. *The Secondary Wall* as the additional wall layers formed within the primary wall. Cells having secondary walls lose their potentiality for growth and enlargement.

In their study of the first cell-walls formed, Kerr and Bailey point out that the so-called middle lamella of earlier workers included at least three distinct layers of the wall: an isotropic intercellular material and two anisotropic layers containing cellulose (the two primary walls). The greater intensity of the double refraction in the first layers of the secondary wall overshadows that of the primary walls which is relatively faint, possibly because of a higher content of colloidal material of pectic nature. Fig. 1 taken from their paper makes clear the layers of the wall that the proposed terms will designate. It is to be hoped that this terminology will be generally accepted so that the terms *middle lamella, primary wall* and *secondary wall* may be used by future workers without danger of being misunderstood.

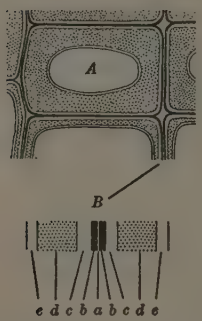


FIG. 1. (From Bailey). (A). Diagrammatic cross-section of a tracheid illustrating the various layers of the wall. (B). Enlarged section of the wall illustrating the terminology applied to the different layers of the wall: (a) middle lamella or intercellular substance, (b) primary walls, (c, d, and e) layers of the secondary wall.

Methods Available for Studying the Structure of the Cell-Wall

The problem of cell-wall structure has been attacked in a number of different ways. Eight or ten different lines of investigation have been used with success and each has added its contribution to the final picture. The modern conception of cell-wall

[2] Isotropic substances appear dark when viewed through crossed-Nicols. Anisotropic substances are visible through crossed-Nicols, assuming different positions in response to light.—Editor.

structure is really a mosaic carefully built from the evidence slowly acquired from various experimental methods. The contributions that each of these methods has made will be briefly outlined.

1. *Direct Observation of Untreated Material.* A great deal may be learned about the structure of the plant cell-wall by merely examining sections cut in different directions. The existence of definite layers in the wall is at once apparent. Surface markings such as striations, radial lines, pits and irregular thickenings frequently suggest the existence of fundamental structural divisions. Further, differences in refractive indices of the different layers indicate the presence of different materials.

2. *Differential Staining.* The existence of specific membrane compounds may be indicated by differential adsorption of certain dyes or by color reactions resulting from specific chemical changes (Plate Fig. 1). Differential staining is an important tool in cell-wall studies if properly used but it is not infallible. Differential adsorption is rarely complete and is markedly influenced by the concentration of the dye, the acidity of the medium, the solvent used and by the presence of unknown substances in the membrane. The experienced worker can gain much information regarding the presence and localization of certain membrane constituents from staining reactions. The recent extensive studies of Czaja (10, 11) upon metachromatic staining indicate that differential staining may also give information regarding the spatial distribution of the submicroscopic units in the wall. Kisser (30) has also shown that physical differences in the wall may cause beautiful examples of the differential adsorption of dyes.

3. *Differential Solubilities.* The presence of different chemical compounds in the wall of the plant cell can be nicely shown through differences in the solubilities of these materials in certain reagents. Copper-oxide-ammonia, for example, will remove unmodified cellulose from the wall without removing cutin, suberin, lignin or pectic materials. Similarly, each of the mentioned wall constituents may be extracted from the wall through the use of suitable solvents. The importance of this method of investigation is illustrated in Anderson's (1, 2, 3) study of collenchyma and epidermal cell-walls, by Lüdtke's (36) work upon fiber cells and by Kerr and Bailey's (29) interesting investigation of the middle lamella. (Plate Figs. 2 and 4).

4. *Polarized Light.* The possibilities of polarized light as a method of investigating the structure of the cell-wall have been well shown in the extensive studies of Frey-Wyssling (17, 18, 19, 20, 28). Polarized light not only permits the detection in the cell-wall of isotropic materials such as pectic compounds and lignin and the localization of anisotropic constituents as cellulose, hemicellulose and cutin, but also furnishes information regarding the spatial orientation of the submicroscopic units that make up the cellulose wall (Plate Fig. 3). The brilliant interference colors produced when a gypsum plate Red I is inserted in the field may be used to detect the location of cutinized lamellae and to indicate the orientation of the submicroscopic units of the wall. When fiber cell-walls are stained with chlorzinc iodide, congo red, Magdala red or certain other dyes they show dichroic phenomena, *i.e.,* they change color when rotated between crossed Nicols. This change in the intensity of color is due to the regular arrangement of the submicroscopic units of the wall (19). Cellulose walls are strongly dichroic, but lignified, cutinized or suberized walls do not show the phenomenon. This offers a method of detecting the early stages of lignification or cutinization in cellulose walls where it is not readily detected in other ways. Polarized light, therefore, permits the exact localization of isotropic lamellae such as the middle lamella in the wall, indicates the presence of crystalline units of submicroscopic size in cellulose, permits the determination of the orientation of these submicroscopic units and finally provides an invaluable method of detecting the lignification and cutinization of the cellulose walls.

5. *Fluorescent Light.* Fluorescence is the phenomenon by which the wave lengths of incident light are reradiated from objects in different wave lengths. The fluorescent light is usually of longer wave length than the incident light. If sections of lignified tissue are radiated with ultraviolet waves which are, of course, invisible to the eye, the tissue will become visible through the fluorescent light. The intensity of the fluorescent light varies with the degree of lignification so the progress of lignification may be followed by observing the tissue, mounted upon a quartz slide, with an ordinary microscope. Künemund (32) states that cambium cells do not fluoresce when wet but that the wood cells show definite fluorescence that increases with age. He was also able to

detect the presence of certain membrane constituents by the different color of their fluorescent light.

6. *X-ray Analysis.* The reflection of X-rays from the regularly arranged molecular groups in the cellulose wall produces spots or lines upon a photographic film placed in a position to intercept the reflected rays. From this spot pattern it is possible to determine the spatial relations of the molecular groupings (48, 49, 50, 51, 52, 53). This method of investigation has been applied to a study of plant cell-wall by numerous investigators and has made possible a determination of the actual size of the molecular aggregates in the wall, their distance from each other and their spatial relationships. It is further evidence that the plant wall is crystalline in nature.

7. *Ash Analysis.* If thin sections of tissue are carefully burned to remove all organic matter the ash will frequently remain in a distinct pattern. The residue of a wall may then be tested microchemically and the minerals present determined. This is of importance in that it is frequently impossible to detect the presence of mineral elements in the intact wall. Czaja (10) has used this method to show that intense staining of walls with ruthenium red may not be associated with the presence of pectic materials as has been generally assumed but is due to the presence of salts of calcium and phosphorous. These substances cannot be detected in the normal cell-wall but ashing the sections reveals their presence.

8. *Spierer Lens.* The Spierer lens differs from the usual oil-immersion objective by having a small mirror of aluminum, gold or silver deposited upon the vertex of the front lens. This mirror reflects some of the light entering the lens from the condensor. If the light from the condensor is stopped down until the beam entering the objective is totally reflected by the mirror, a dark field is produced. The light is reflected from the mirror to the object under examination and is again reflected from the surface of the object and enters the objective through the portion of the lens that is not covered by the mirror. The image produced by this lens consists of numerous alternating light and dark striations. In some instances the striations are broken up into short rods or irregularly shaped objects. This image has been variously interpreted. Seifriz (43, 45), who called attention to the lens and to

the unusual images that it produced, suggested that the Spierer image indicated the presence of definite structural units of ultramicroscopical dimensions. He contended that the Spierer lens provided further evidence for the micellar structure of the cellulose cell-wall. Thiessen (54) used the Spierer lens in studying the decomposition of the cell-walls of woods in relation to the structure of lignite and coal. The striations were assumed to be evidence of the existence of definite micelles. The essential similarity in the images produced by sections of sound and rotted wood cell-walls was considered by Thiessen as sufficient evidence for the existence of some close relationship between cellulose and lignin. The similarities in the Spierer images of thin sections of coal and those of cellulose membrane was considered to be evidence of the persistence in coal of the original cell-wall structure of the plants from which the coal was formed. These conclusions as well as those of Seifriz must be critically regarded in consequence of the recent investigations of Clifford and Cameron (8). These investigators show that the Spierer image is probably the result of diffraction phenomena. Certainly it is no longer possible to accept measurements based upon Spierer images as indicating structural units characteristic of the material under observation, since similar images were obtained from such diverse substances as cotton fibers, asbestos fibers, salicylic acid crystals, iron wire and even from the lines on a stage micrometer (Plate Figs. 7 and 8).

Collenchyma cell-walls are known to consist of alternate lamellae of cellulose and pectic compounds. Either of these substances can be removed from the wall leaving the other remaining. Clifford and Cameron examined untreated collenchyma walls with the Spierer lens and then compared with this image the images obtained from collenchyma cell-walls from which cellulose or pectic materials had been removed. The same Spierer image was obtained in each case; no relation between the Spierer image and the structure of the wall could be detected. Berkley (6), in his recent study of the structure of wood, used the Spierer lens to bring out the gross structure of the wall but reported that he was unable to confirm the observations of Seifriz and Thiessen upon the presence of diffraction patterns of micellar aggregates in Spierer images. It seems highly probable, therefore, that the

Spierer image has little or no significance so far as indicating the presence of fundamental structural units.

9. *Measurements of Refractive Indices.* Much may be learned about the structure of the wall from the refractive indices of the various lamellae. By mounting sections of tissue in liquids of varying refractive index the prominence of certain portions of the wall is greatly emphasized while that of other wall areas is diminished. This indicates the presence and gives the localization of different membrane materials.

10. *Hydration.* By the use of suitable reagents the wall of the cell may be greatly swollen. In the swollen condition, structural relations appear that are invisible in the unswollen state (Plate Figs. 4, 5, 6). Ball (5) has been able to count the layers present in a cotton fiber by using this method and to show some correlation between the number of layers and the number of day and night periods during which secondary thickening occurred. Sakostschikoff and Korsheniousky (41) were able to use this method to make counts of the layers in the cotton fiber but were unable to confirm Ball's theory of the origin of the layers since they found no consistent relation between the age of the fiber and the number of lamellae.

This brief description of the various methods employed by cell-wall investigators furnishes some idea of the way in which the data, upon which modern ideas of wall structure are based, have been obtained.

The Fine Structure of the Cell-Wall

Three different conceptions of the fine details of cell-wall structure are current at the present time. The three ideas have certain features in common but differ in regard to the supposed size of the structural units of the wall.

The most widely held idea of the structure of the cellulose cell-wall does not differ essentially from the original Nägeli hypothesis. The important investigations of Frey-Wyssling (17, 20) with polarized light and those of Meyer (37), Meyer and Mark (38), Herzog (26), Clark (7) and others with the X-ray, indicate that the wall is composed of submicroscopic elongated units or micelles of crystalline nature. These crystalline micelles are separated from each other by a hydrophilic colloidal material. Figure 2B

from Seifriz (43) illustrates well the supposed arrangement of these micellar units. The crystalline character of the micelles is indicated by their double refraction between crossed Nicols.

Double refraction may be caused by the regular orientation of small isotropic rods imbedded in some medium. When the refractive index of the rods is equal to that of the surrounding medium, the system of rods and medium becomes isotropic. The cellulose wall of plant cells is doubly refractive when saturated with a series of liquids of varying refractive indices thus indicating that the double refraction is due to the crystalline nature of the micelles themselves and not to their orientation in the wall. This is confirmed by the results of X-ray studies for they also offer evidence of the existence in the wall of submicroscopic crystalline units. The presence of an intermicellar colloidal substance capable of swelling is evidenced by the swelling of the wall in water. In the swollen condition X-ray pictures show that the micelles themselves do not change in size but that distance between the micelles has increased. If the swelling of the wall were due, as Nägeli supposed, to the formation of adsorbed films of other films of water around the micelles, liquids such as ether and chloroform should likewise form films around the surfaces of the micelles and should cause some swelling. The failure of the cell-wall to swell when immersed in such organic liquids supports the idea that swelling is not due to the formation of liquid films around the micelles but to the presence of some intermicellar material of hydrophilic character. X-ray investigations also indicate the presence of some intermicellar material (26).

The internal structure of the micelle is also revealed by X-ray analysis. The basic cellulose group appears to be a long chain of glucose residues (glucose minus one molecule of water). A portion of one such chain consisting of two glucose residues is illustrated in Fig. 2A. The length of the chain is variously estimated by different investigators. Meyer (37) considers the chain to be composed of from 50–80 glucose residues. Freudenberg (16) estimates that the chains contain from 100–200 glucose units while Sponsler (48, 49, 50) considers the chains to be of indefinite length containing hundreds or even thousands of glucose units. The chain-like cellulose "molecules" are grouped into bundles in which they are arranged in parallel rows. These bundles of parallel

chains of glucose residues (cellulose "molecules") form the micelles. The number of parallel chains present in a single micelle is estimated by Meyer (37) to be from 40–60, by Freudenberg (16) to be about fifty. The micelle is the smallest morphological unit of natural cellulose. Meyer assigns a length of 15–30 mμ[3] and a diameter of 2–5 mμ to these micellar units. Herzog estimates the micelles of hemp fiber to be 11.7 mμ long and 6.6 mμ in diameter, while Freudenberg considers the units in natural cellulose to have a size range of 50–100 mμ in length and a diameter range of about 6 mμ.

It is probable that not all of the micelles are of identical size in the same wall and probably the chains of glucose residues vary in size. So it is not possible to speak of cellulose molecules in the strict sense of the word. It is impossible that the celluloses in different species or even in different walls of the same individual organism are identical in their structural organization.

It is interesting to note that solutions of cellulose contain micelles of essentially the same size as those in the solid cell-wall (37). Various mechanical or chemical treatments may alter the size of the micellar units. Artificial fibers formed from solutions of cellulose show micelles of smaller size than those in the original native raw material (7). It seems probable that one reason for the lower tensile strengths of such artificial fibers is this decrease in the size of the micellar units.

The forces that hold the glucose residues together in long chains are the primary valence forces while the forces holding the chains together in the micelle are of the same order as those forces holding together the molecular aggregates of organic crystals—the forces of molecular cohesion. These can be measured in calories and Meyer (37) estimates that the forces in the case of a chain of fifty glucose residues amounts to about 1,200,000 calories. These tremendous forces, considerably greater than those holding the atoms together within the molecule, bind the chains of glucose residues together and are effective at the surface of the micelles themselves, there serving to bind the micelles together.

The micelles composing the wall are grouped into long fibrils in the case of fiber cells and these fibrillar units may be parallel

[3] mμ = one one-thousandth of a micron; micron = one one-thousandth of a millimeter.

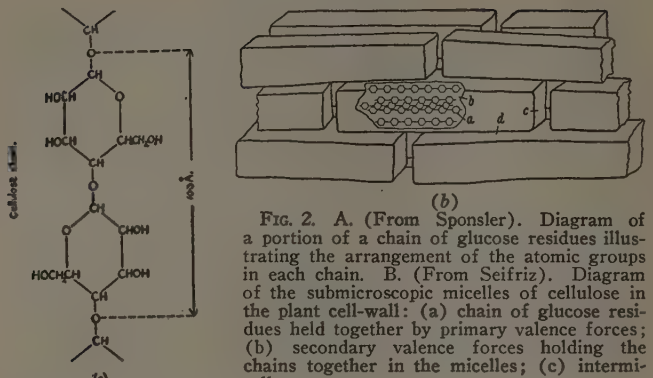


FIG. 2. A. (From Sponsler). Diagram of a portion of a chain of glucose residues illustrating the arrangement of the atomic groups in each chain. B. (From Seifriz). Diagram of the submicroscopic micelles of cellulose in the plant cell-wall: (a) chain of glucose residues held together by primary valence forces; (b) secondary valence forces holding the chains together in the micelles; (c) intermicellar spaces.

or inclined to the long axis of the fiber cell (Plate Figs. 5, 6). The angle of their inclination varies in different layers in the wall and may reverse its direction in the same layer of the wall as in the case of cotton (20). In some fiber cells the direction of the spiral fibrils is reversed in successive layers in the wall giving an alternation of right- and left-handed spirals in successive lamellae. Clark (7) reports that the angle of these spiral fibrils differs in compression wood from that in wood not subjected to compression. Jaccard and Frey (28) report a similar difference in the micellar orientation of wood under tension and that under compression. The latter investigators point out the rather surprising fact that this effect of tension and pressure was limited to the woody fibers and was not observed in the water conducting elements. The arrangement of the micelles in the bordered pits of coniferous wood has been reported by Frey (18, 20) as being that of concentric circles. This has been confirmed by the X-ray observations of Ritter (40). Frey reports a wide range of micellar orientation in the walls of different tissues (20).

Evidence of a different kind supporting the micellar hyopthesis of cell-wall structure is presented by the studies of Gurewitsch (21) upon the permeability of the seed coats of certain seeds. The changes in the permeability of the cell-wall were explained in terms of alterations in the orientation of the micellar units in the wall especially as regards the size of the intermicellar spaces. The

presence of a hydrophilic intermicellar material is also indicated by the change in permeability produced by different reagents.

Czaja (10, 11), in extensive studies of metachromatic staining, finds that the micellar hypothesis adequately accounts for the differential staining obtained. Künemund (37), using metachromatic staining as evidence, describes variations in the size of the micellar units and differences in the size of the intermicellar spaces during lignification.

The second conception of cellulose cell-wall structure is that of Sponsler (48, 53) who was one of the first to apply X-rays to an analysis of fiber cell-walls. He differs from the other X-ray workers cited in that he considers the X-ray evidence in support of the existence of micelles as definite entities in the wall, to be inadequate. Refraction patterns giving the impressions of micellar units may be the result of bending or warping of the material under examination. To quote (48): "It seems, then, that the very minute warped and bent regions in organized structures might readily be mistaken for individual blocks and measured by X-ray methods for micelles." Sponsler considers the wall to be composed of long parallel chains of glucose residues running lengthwise of the fiber. The chains are oriented in such a way as to form a space lattice of three dimensions. Figure 3C shows the arrangement of the glucose residue units in the space lattice. This arrangement forms a unit group that is 6.10×

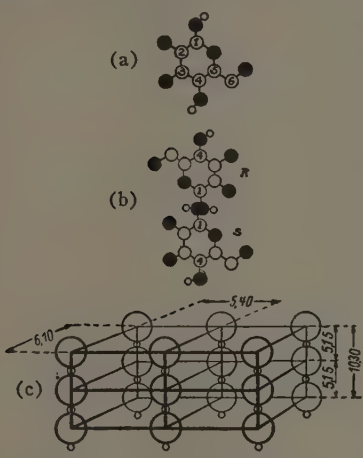


FIG. 3. (From Sponsler). (A). Diagram of the orientation of the atomic groups in a single glucose residue. Numbered circles represent carbon atoms; solid circles represent oxygen atoms; only two hydrogen atoms are shown. (B). Two glucose molecules placed as they are oriented in the cellulose chain to show the position of the OH groups at the time of condensation. Hydrogen atoms are represented by the small circles. (C). Spatial arrangement of the chains of glucose residues. Three glucose residue units in six different chains are illustrated. The dimensions are given in Angstrom units.

5.40 × 10.30 A.U. (An Angstrom Unit is 0.1 mμ). In this diagram two vertical layers of chains are shown at right angles spaced 6.10 A.U. apart. The chains of glucose residues are spaced 5.40 A.U. apart in each layer. At right angles to these vertical chains, that is, in the horizontal position, three more layers of chains are shown spaced 5.15 A.U. apart. In the cellulose walls of fiber cells three planes of glucose residues are present. In ramie fiber the planes across the fiber are about at right angles with the fiber axis but this angle varies in other walls.

From this pattern it will be seen that the cellulose wall is considered to be a complex system built up of very thin molecular layers each composed of long chains of glucose residues. The surface view of one such layer is shown in Fig. 4. Certain

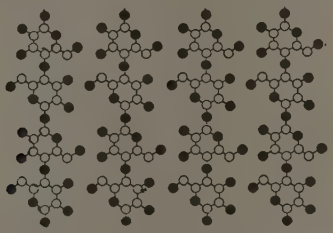


FIG. 4. (From Sponsler). Surface view of glucose residue chains forming one layer in the cellulose wall. The white circles represent carbon atoms, the black circles represent oxygen atoms.

layers extend lengthwise of the fiber wall, some extend across the wall and other layers form definite angles with the lengthwise layers. In the cylindrical fiber cell-wall the radial layers of chains are spaced 5.40 A.U., the tangential layers 6.10 A.U. and the vertical layers 5.15 A.U. from the center of one glucose residue to the center of the next adjacent residue. A single fiber cell-wall may be some 40,000 of these unit cell lattices in thickness. The wall of a fiber cell consists, then, according to Sponsler, of an enormous number of parallel molecular layers and not of a system of brick-like units as suggested by the micellar hypothesis.

Sponsler (50) suggests that since the inner surface of the wall adjacent to the protoplasm has a definite molecular pattern, the forces of crystallization at this surface may form a part of the mechanism by which glucose molecules become converted into cellulose (Fig. 3D).

The markings visible in cross-sections of fiber cells and upon the surface of the cell-wall bear no relation to the orientation of the glucose residue groups.

The third idea of cell-wall structure is that the wall is composed of definite cellulose units of visible size, each unit being enclosed in a thin film of non-cellulose material which serves to cement the units together. This concept has been supported by Lüdtke (36), Hess (27) and more recently by Farr and Eckerson (12, 13). Figure 5 is taken from a recent paper of Lüdtke (36) and illustrates his conception of cell-wall structure. The wall is built, according to this theory, in segments separated by definite cross elements. The lamellae so characteristic of thickened walls are believed to be caused by very thin films of non-cellulose material enclosing the cellulose itself. The vertical striations in the wall are similarly believed to be the result of thin films of non-cellulose material enclosing bundles of spiral fibrils. These thin films of non-cellulose material serve to act as a glue binding the cellulose segments together in the wall. The nature of the material composing these films apparently varies in different walls but the same structural system exists. The evidence for this structural system is based upon the behavior of cell-walls during swelling and solution in various reagents and upon the reaction of the fiber cells to certain dyes, especially chlorzinc iodide. This dye frequently fails to give the characteristic blue color when added to cellulose walls unless the wall is subjected to mechanical pressure. The application of this pressure, according to Lüdtke, ruptures the thin non-cellulose film surrounding the cellulose and permits the staining reagents to reach the cellulose.

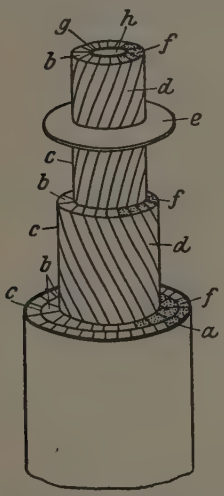


FIG. 5. (From Lüdtke). Diagram of a small segment of a cellulose fiber cut away to illustrate the structure of the wall: (a) The primary cell wall. (b) Layers of the secondary wall. (c) Thin films of non-cellulose material separating the layers in the wall. (d) Spirally wound bundles of fibrils. (e) Cross element separating the fiber wall into segments. (f) Fibrils composing the spiral elements. (g) Innermost layer of the wall. (h) Cell lumen.

quently fails to give the characteristic blue color when added to cellulose walls unless the wall is subjected to mechanical pressure. The application of this pressure, according to Lüdtke, ruptures the thin non-cellulose film surrounding the cellulose and permits the straining reagents to reach the cellulose.

The recent papers of Farr and Eckerson (12, 13) seem to give additional support to this conception of cell-wall structure. They find that visible anisotropic crystalline particles can be demonstrated in the cell-wall and that by removal of "non-cellulose cementing materials" from cellulose particles with strong hydrochloric acid large numbers of cellulose particles can be obtained. They do not report the existence of any cross elements in the fiber wall, but their conception of a wall formed by the cementing together of definite cellulose particles with some non-cellulose substances suggests a membrane structure somewhat similar to the more elaborate plan advanced by Lüdtke.

Farr and Sisson (14), in a recent paper, suggest that the visible cellulose units reported by Farr and Eckerson may satisfactorily account for the X-ray patterns formerly thought to be the result of the existence of micellar units.

Hess (27) likewise describes the presence of "Blättchen" in the wall of cellulose fibers. He gives their size as ranging from 75–100 μ and suggests that these cellulose particles may be surrounded by thin films of non-cellulose material. He further points out that the X-ray diagrams of cellulose are better when the material is not thoroughly purified and freed from non-cellulose constituents indicating the orienting influence of the non-cellulose films. Hess is convinced that a system of films such as pictured by Lüdtke is an important structural feature of the fiber wall and bears a direct causal relationship to many of the properties of cellulose fibers.

Modifications of Cellulose Walls

Cellulose is not known to occur in plant cell-walls unaccompanied by other materials. The most widely studied modification of the cellulose wall is the change known as lignification that occurs in woody and other tissues. Lignin is an amorphous substance of unknown chemical composition that appears in many cell-walls that undergo secondary thickening. The first evidence of lignifica-

tion appears in the middle lamella where the pectic compounds are intensely lignified. Whether this change involves a partial transformation of the pectic material of the middle lamella into lignin or whether lignin is merely added to the pectic material already present, masking its appearance, is not definitely known. The careful work of Kerr and Bailey (29) has shown that both lignin and pectic material are present in the intensely lignified middle lamella of woody tissue. Kerr and Bailey show that Ritter's (40) conception of a middle lamella largely composed of lignin is based upon an objectionable method of removing lignin from the wall. Harlow (22, 25), in a series of papers, has also supported the idea that most of the lignin in wood is located in the middle lamella but further emphasizes that the presence of lignin need not exclude the presence of pectic materials. In a study of the lignification of wood cells Scarth *et al.* (42) found varying amounts of lignin in various portions of the wall with the greatest amount in the middle lamella. They were unable to demonstrate the presence of either cellulose or pectic materials in the middle lamella but were also unable to demonstrate the absence of these materials.

Lignin is present also in the secondary layers of the wall but Ritter (40), Harlow (22) and others have reported chemical and physical differences between the lignin of the middle lamella and that of the secondary layers of the wall. Lüdtke (36) considers that lignin is limited to the middle lamella and that the substance in the secondary wall generally classed as lignin is not lignin but a chemically different material that forms the thin films enclosing the cellulose constituents of the wall. The lignin of the secondary wall, if it is lignin, gives some but not all of the color reactions characteristic of the lignin of the middle lamella and differs in its resistance to solvents.

Lignification of cellulose walls does not alter the X-ray patterns of cellulose, so lignin does not involve a modification of the cellulose units themselves. In view of the dichroic effects of lignification (19) and the fact that either lignin or cellulose may be removed from a lignified wall without altering the structural relation of the other material, it seems probable that lignin is deposited between the cellulose micelles and involves a change in the intermicellar material rather than a change in the micelles themselves.

The process of lignification has been carefully studied in a variety of ways. Künemund (32), using metachromatic staining and fluorescent light, reports alterations in the micellar organization of the wall during lignification. The intermicellar spaces seem to vary in size. Kisser (30) also reports evidences of physical changes of the wall during lignification on the basis of the differential adsorption of certain dyes.

Freudenberg (16) considers two kinds of lignin: (a) primary lignin consisting of definite structural units formed in physiological synthesis and (b) secondary lignin built up from the chains of primary lignin to form large irregular three dimensional formations. The secondary lignin is considered to be a post-mortem condensation product of primary lignin. Hemicellulose is believed to be present with the lignin in the wall but neither compound is considered to penetrate the cellulose micelle, so most of the cellulose chains make no contact with the lignin in the wall.

Pectic compounds seem very commonly associated with cellulose in plant cell-walls. They may occur in definite lamellae in wart-like accumulations between cells (31) or may permeate the intermicellar spaces of the cellulose portions of the wall. Removal of cellulose with ammoniacal-copper-oxide from certain cell-walls leaves the pectic materials unaffected and in many cases the cell-wall appears unchanged in thickness, indicating that pectic materials have permeated the cellulose structure. Removal of the pectic material usually brings about a striking lamellation of the wall which suggests that definite lamellae composed largely or entirely of pectic material were present between the cellulose lamellae (1).

The striking affinity of pectic compounds for ruthenium red has made this dye a favorite test for the presence of pectic compounds. Kerr and Bailey (29), after a critical examination of this dye, find that while it is not specific for pectic materials it may be used with certain precautions as a strongly presumptive test for those compounds. Czaja (10) has reported evidence, however, to indicate that the adsorption of ruthenium red by tissues is no indication of the presence of pectic compounds but that it is determined by the presence of organic salts of calcium and phosphorous.

Pectic compounds make up the first cell-wall formed between the daughter nuclei, and subsequent layers of cellulose wall con-

tain more or less pectic material. As indicated earlier, pectic material is the first to be lignified and this has led to the suggestion that lignification is, in part at least, a change of pectic material in the wall.

Cutinized cell-walls have also been the subject of considerable study. Lee and Priestly (33) suggest that cutin reaches to the surface of epidermal cell-walls by migrating along the radial walls of subepidermal tissue. At the surface, exposure to light and oxygen bring about chemical and physical changes that produce the cuticle. Frey (18, 20) and Anderson (2) have shown that complicated relations between cutin, pectic materials and cellulose lamellae exist in certain epidermal walls. In some cases cutinized cellulose lamellae are deposited adjacent to the living protoplasm on the *inner* face of the outer epidermal wall (3). This suggests that cutin may be formed by the protoplasm of the epidermal cell itself and that cutinization of epidermal walls may not be directly related to exposure to dry air, light and oxygen.

Cell-walls are usually regarded by botanists as non-living structures produced by the living protoplast. There is evidence, however, that indicates a more active rôle for the cell-wall. Lloyd (34), in describing reproduction in a species of *Spirogyra,* observed that the bulging of the female gamete was not due to internal pressure but to changes in the wall itself. As a result of these observations Lloyd says, "Whatever the minutiae involved may be, it would seem that we are forced to recognize that there are qualities of the cell-wall in the living cell which may change—such change constituting a behavior of the cell as a living whole. In some measure we may assert the wall itself to be a living part of the cell." In another paper Lloyd and Ulehla (35) find that in the marine alga *Postelsia* some irreversible change similar to death occurs not only in the protoplast but also in the cell-wall.

Studies of the growth of cell-walls indicate that, in some cases at least, turgor pressure may not be the cause of the extension of the wall. Söding (47), in his study of cell-wall extensibility, finds that the first stages of cell-wall growth are not caused by turgor pressure. This point of view is disputed by other investigators. Cranner (9) considered the wall as a living structure and believed the outer layers of the protoplasm were continuous with the intermicellar substance. While the possibility of vital

activity in the cell-wall cannot be denied, the evidence in support of this contention is inadequate at present to warrant its general acceptance.

The writer has attempted to call attention to recent developments and at the same time to convey some picture of the cell-wall as it appears to workers in the field. Many problems of cell-wall structure are still the subject of active discussion and debate and further discoveries may bring changes of greater or lesser magnitude to the ideas now current. A few generalizations may be safely made from facts so far accumulated:

1. The cell-wall is a laminated structure composed of many lamellae that differ in chemical and physical properties.
2. The skeletal framework of the walls of the higher plants is composed of cellulose.
3. Cellulose is composed of long parallel chains of glucose residues. These chains are definitely oriented in the wall but the exact method of their orientation is a matter of dispute.
4. The cellulose framework of the wall is permeated with non-cellulose materials of amorphous character.
5. It is possible that the plant cell-wall may possess some of the characteristics usually attributed to living material during certain phases of its growth.

The writer wishes to acknowledge his indebtedness to Professor Dr. J. Kisser of Vienna for calling his attention to certain papers of interest and importance.

References

1. Anderson, D. B. Über die Struktur der Kollenchymzellwand auf Grund mikrochemischer Untersuchungen. Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss Kl., Abt. I, **136**: 429–439. 1927.
2. ————————. Struktur und Chemismus der Epidermis-Aussenwand von *Clivia nobilis*. Jahrb. wis. Bot. **69**: 501–515. 1928.
3. ————————. The distribution of cutin in the outer epidermal wall of *Clivia nobilis*. Ohio Jour. Sci. **34**: 9–18. 1934.
4. Bailey, I. W. The cambium and its derivative tissues. Am. Jour. Bot. **10**: 499–509. 1923.
5. Ball, W. L., and Hancock, H. A. The existence of daily growth rings in the cell-wall of cotton hairs. Proc. Royal Soc. London **90**: 542–554. 1919.
6. Berkley, E. E. Certain physical structural properties of three species of Southern yellow pine correlated with compression strength of their wood. Ann. Mo. Bot. Garden **20**: 339–342. 1934.

7. Clark, G. L. Cellulose as it is completely revealed by X-rays. Jour. Ind and Eng. Chem. **22**: 174–487. 1930.
8. Clifford, A. T., and Cameron, F. K. Dark-field studies of fibers Ind. and Eng. Chem. **26**: 1209–1213. 1934.
9. Cranner, Hansteen B. Untersuchungen über die Frage ob in der Zellwand lösliche Phosphatide vorkommen. Planta **2**: 438–445. 1926.
10. Czaja, A. Th. Untersuchungen über metachromatische Farbungen von Pflanzengeweben II. Planta **21**: 531–601. 1934.
11. ————. Untersuchungen über metachromatische Farbungen von Pflanzengeweben I. Planta **11**: 582. 1930.
12. Farr, W. K., and Eckerson, S. Formation of cellulose membranes by microscopic particles of uniform size in linear arrangement. Contrib. Boyce Thompson Inst. **6**: 189–203. 1934.
13. ————. Separation of cellulose particles in membranes of cotton fibers by treatment with hydrochloric acid. Contrib. Boyce Thompson Inst. **6**: 309–313. 1934.
14. Farr, W. K., and Sisson, W. A. X-ray diffraction patterns of cellulose particles and interpretation of cellulose diffraction data. Contrib. Boyce Thompson Inst. **6**: 315–321. 1934.
15. Farr, W. K., and Clark, G. L. Cotton Fibers II. Contrib. Boyce Thompson Inst. **4**: 273–295. 1932.
16. Freudenberg, K. The relation of cellulose to lignin in wood. Jour. Chem. Ed. **9**: 1171–1180. 1932.
17. Frey, A. Der heutige Stand der Micellartheorie. Ber. deut. bot. Ges. **44**: 564–570. 1926.
18. ————. Die submikroskopische Struktur der Zellmembran. Jahrb. wis. Bot. **65**: 195–223. 1925.
19. ————. Das Wesen der Chlorzinkjodreaktion und das Problem des Faserdichroismus. Jahrb. wiss. Bot. **67**: 597–634. 1927.
19a. ————. Über die intermicellar-Räume der Zellmembranen. Ber. deut. bot. Ges. **46**: 444–456. 1928.
20. Frey-Wyssling, A. Mikroskopische Technik der Micellarunterschung von Zellmembranen. Zeitschr. wis. Mikrosk. **47**: 1–46. 1930.
21. Gurewitsch, A. Untersuchungen über die Permeabilität der Hülle des Weizenkorns. Jahrb. wis. Bot. **70**: 657–706. 1929.
22. Harlow, W. H. Further studies on the location of lignin in the cell-wall of wood. Am. Jour. Bot. **19**: 729–739. 1932.
23. ————. Microscopy of acid-treated sawdust as an index to some of the differences in the physical properties of hardwood and soft-wood lignin. Ind. and Eng. Chem. **23**: 419. 1931.
24. ————. Lignification in the secondary and tertiary layers of the cell-walls of wood. Bull. N. Y. State Coll. For. Tech. Pub. No. 24. 1928.
25. ————. The chemical nature of the middle lamella. N. Y. State College For. Tech. Pub. No. 21. 1927.

26. Herzog, R. O. Zur Erkenntnis der Cellulose Faser. Ber. deut. Chem. Ges. **58**: 1254–1262. 1925.
27. Hess, K. Zur Frage des Aufbaues pflanzlicher Membran. Biochem-Zeitschr. **203**: 409–420. 1928.
28. Jaccard, P., and Frey, A. Einfluss von mechanischen Beanspruchungen auf die Micellarstruktur, Verholzung und Lebensdauer der Zug- und Druckholzelemente beim Dichenwachstum der Bäume. Jahrb. wis. Bot. **58**: 844–866. 1928.
29. Kerr, T., and Bailey, I. W. Structure, optical properties and chemical composition of the so-called middle lamella. Jour. Arnold Arbor. **15**: 327–349. 1934.
30. Kisser, J. Zur Färbung kutinisierter Zellulose-Membranen. Zeitschr. wis. Mikrosk. **45**: 163–171. 1928.
31. ————. Untersuchungen über das Vorkommen und die Verbreitung von Pektinwarzen. Jahrb. wis. Bot. **68**: 206–232. 1928.
32. Künemund, A. Die Entstehung verholzter Lamellen. Bot. Archw. **34**: 462–521. 1932.
33. Lee, B., and Priestley, J. H. The plant cuticle I. Ann. Bot. **38**: 525–545. 1924.
34. Lloyd, F. E. Additional studies on *Spirogyra*. Trans. Roy. Soc. Can. **20**: Sec. V. 75–112. 1926.
35. Lloyd, F. E., and Ulehla, V. The rôle of the wall in the living cell as studied by the auxographic method. Trans. Roy. Soc. Can. **20**: Sec. V. 45–73. 1926.
36. Lüdtke, M. Untersuchungen über Aufbau und Bildung der pflanzlichen Zellemembran und ihre stofflichen Komponenten. Biochem. Zeitschr. **233**: 1–57. 1931.
37. Meyer, K. H. Die Chemie der Micelle und ihre Anwendung auf biochemische und biologische Probleme. Biochem. Zeitschr. **208**: 1–31. 1929.
38. Meyer, K. H., and Mark, H. Über den Bau des kristallinen Anteils der Zellulose. Ber. deut. chem. Ges. **61**: 593—. 1928.
39. Nägeli, C. Über den inneren Bau der vegetabilischen Zellmembranen. Sitzber. Bay. Akad. Wis. München **1**: 282–323. 1864. **2**: 114–171. 1864.
40. Ritter, G. J. Composition and structure of the cell-wall of wood. Jour. Ind. and Eng. Chem. **20**: 941–945. 1928.
41. Sakostschikoff, A. P., and Korsheniovsky, G. A. Der Entwicklungsgang des Baumwollhaares. Faserforschung **9**: 249–284. 1932.
42. Scarth, G. W., Gibbs, R. D., and Spier, J. D. The structure of the cell-wall and the local distribution of the chemical constituents. Trans. Roy. Soc. Can. Sec. V: 269–288. 1929.
43. Seifriz, W. The origin, composition and structure of cellulose in the living plant. Protoplasma **21**: 129–159. 1934.
44. ————. The contractility of protoplasm. Am. Nat. **63**: 410–434. 1929.

45. ————. The Spierer lens and what it reveals in cellulose and protoplasm. Jour. Phys. Chem. **35**: 118–129. 1931.
46. Sharp, L. W. Introduction to cytology. 3 Ed. New York. 1934.
47. Söding, H. Über das Streckungswachstum der Zellwand. Ber. deut. Bot. Ges. **50**: 117–123. 1932.
48. Sponsler, O. L. The molecule in biological structures as determined by X-ray methods. Quart. Rev. Biol. **8**: 1–30. 1933.
49. ————. Orientation of cellulose space lattice in the cell-wall. Protoplasma **12**: 241–254. 1930.
50. ————. Mechanism of cell-wall formation. Plant Phys. **4**: 329–336. 1929.
51. ————. The molecular structure of the cell-wall of fibers. Am. Jour. Bot. **15**: 525–536. 1928.
52. ————. Molecular structure of plant fibers determined by X-rays. Jour. Gen. Phys. **9**: 677–695. 1926.
53. ————. The structure of ramie cellulose as derived from X-ray data. Colloid Symposium Mono. **4**: 174–202. 1926.
54. Thiessen, R. Physical structure of coal, cellulose fiber and wood as shown by Spierer lens. Ind. and Eng. Chem. **24**: 1032–1041. 1932.

EXPLANATION OF THE PLATE

FIG. 1. Outer epidermal wall of *Clivia nobilis* stained with Sudan III to show the distribution of cutin in the wall. Dark areas are cutinized cellulose, light area is composed of cellulose and pectic compounds (440×).

FIG. 2. Outer epidermal wall of *Clivia nobilis* saponified with hot KOH to remove cutin. Cellulose lamellae over each cell become visible and the lamellation of the innermost cutinized region becomes apparent. Cuticle resists saponification (440×).

FIG. 3. Outer epidermal wall of *Clivia nobilis* between crossed Nicols. The isotropic pectic materials in the wall appear as dark lines. The structural organization of the wall is revealed (500×).

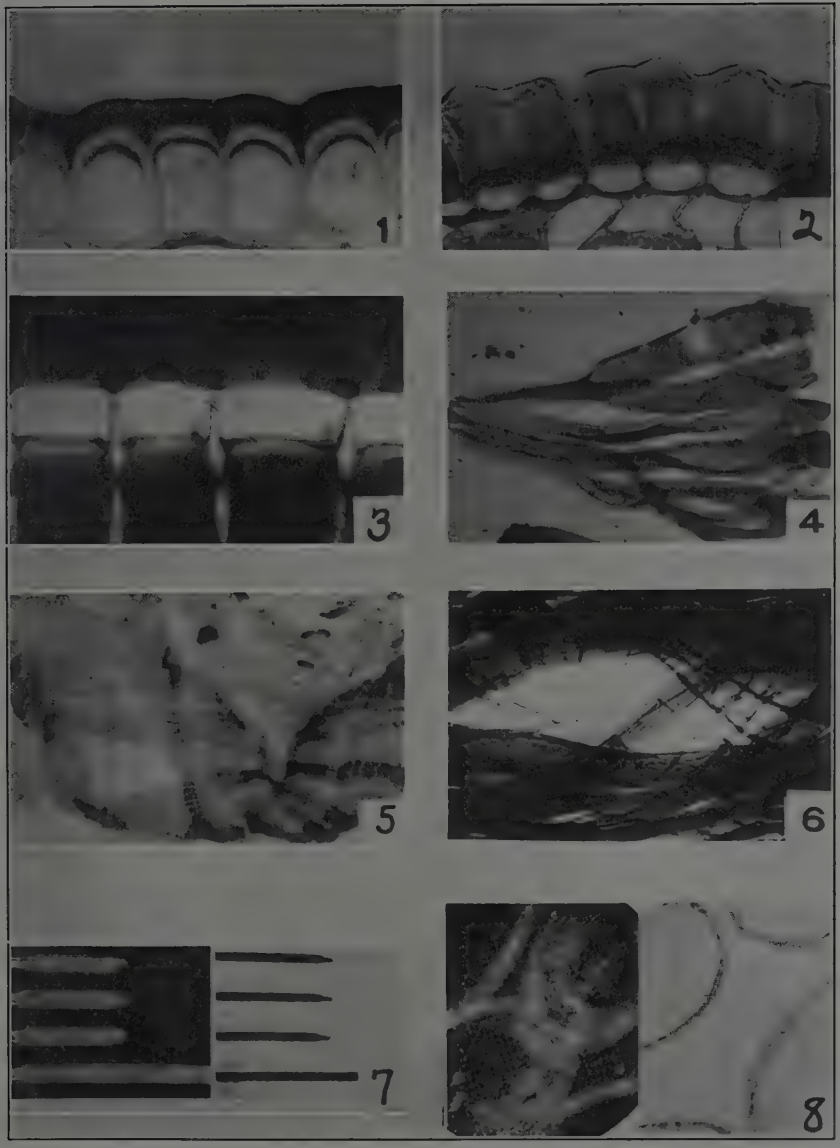
FIG. 4. Small segment of a collenchyma cell-wall of *Lycopersicum esculentum*. Swollen and subjected to pressure. The cellulose lamellae composing the wall have been separated and flattened out (300×).

FIG. 5. Flax fiber swollen to reveal spiral fibrils composing the wall.

FIG. 6. Small segment of one flax fiber wall swollen and subjected to pressure (350×) to reveal its fibrillar structure. The swelling treatment has made the fibrils of the wall large enough to be seen (2000×).

FIG. 7. (From Clifford & Cameron). A stage micrometer as seen through the ordinary oil-immersion microscope objective (950×) and as seen through the Spierer Lens (850×).

FIG. 8. (From Clifford & Cameron). Cross section of the collenchyma cell-walls of *Cyclamen persicum* as seen with ordinary oil-immersion objective (950×) and with the Spierer Lens (890×).


1
2
3
4
5
6
7
8

Natural Convergence of Eyes maintained by SPENCER WIDE-FIELD MICROSCOPE

●

Eliminates Eyestrain . . Increases Comfort

THE Spencer Wide-field Binocular Microscope is the only one in which the prisms are arranged to permit the axes of the oculars to converge at an angle of 8° which is the normal angle of convergence of the eyes at convenient reading distance.

Folder M-55 gives complete description and prices of the Spencer series of Wide-field Binocular Microscopes. We will be pleased to send you a copy.

This exclusive patented Spencer feature is one of great importance to one whose work necessitates the constant use of a wide-field microscope. The ordinary construction requires a convergent angle of the eyes of 16° which imposes an eyestrain that is excessive. The intensive eyestrain from working at this ocular convergence angle of 16° is eliminated . . and it just naturally results in protection for the eyes and increased comfort for the observer.

Spencer Lens Company

BUFFALO NEW YORK

BROOKLYN BOTANIC GARDEN MEMOIRS

Volume I: 33 contributions by various authors on genetics, pathology, mycology, physiology, ecology, plant geography, and systematic botany. Price, $3.50 plus postage.

Volume II: The vegetation of Long Island. Part I. The vegetation of Montauk, etc. By Norman Taylor. Pub. 1923. 108 pp. Price $1.00.

Vol. III: The vegetation of Mt. Desert Island, Maine, and its environment. By Barrington Moore and Norman Taylor. 151 pp., 27 text-figs., vegetation map in colors. June 10, 1927. Price, $1.60.

AMERICAN JOURNAL OF BOTANY

Devoted to All Branches of Botanical Science

Established 1914. Monthly, except August and September. Official Publication of the Botanical Society of America. Subscriptions, $7 a year for complete volumes (Jan. to Dec.). Parts of volume at the single number rate. Volumes 1–21 complete, as available, $170. Single numbers, $1.00 each, post free. Prices of odd volumes on request. Foreign postage: 40 cents.

ECOLOGY

All Forms of Life in Relation to Environment

Established 1920. Quarterly. Official Publication of the Ecological Society of America. Subscription, $4 a year for complete volumes (Jan. to Dec.). Parts of volumes at the single number rate. Back volumes, as available, $5 each. Single numbers, $1.25 post free. Foreign postage: 20 cents.

GENETICS

A Periodical Record of Investigations bearing on Heredity and Variation

Established 1916. Bi-monthly.

Subscription, $6 a year for complete volumes (Jan. to Dec.). Parts of volumes at the single number rate. Single numbers, $1.25 post free. Back volumes, as available, $7.00 each. Foreign postage: 50 cents.

Orders should be placed with

The Secretary, Brooklyn Botanic Garden

1000 Washington Ave., Brooklyn, N. Y., U. S. A.

Turtox Botanical Slides

A catalog of practical interest to every teaching botanist

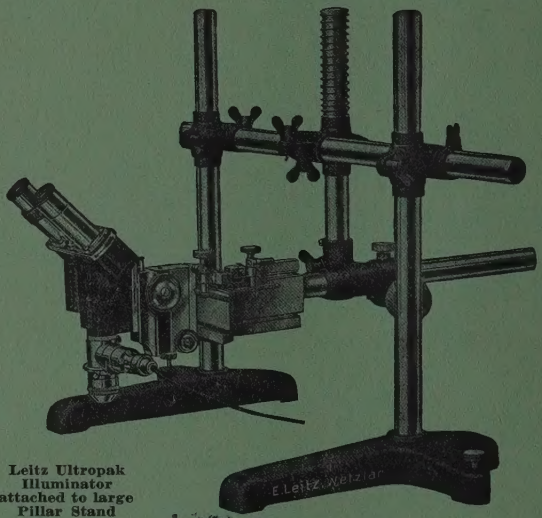
In the Turtox Microscope Slide Catalog No. 34, over seventy-five pages are devoted to descriptions and illustrations of dependable microscope slides for bacteriology, botany and cytology. Teachers will be particularly interested in the large number of life history groups and other economical sets of slides, as well as in the many striking demonstration preparations described in the cytology section.

If you do not have this Turtox Catalog, write today for your copy. Please indicate your professional position and mention The Botanical Review.

The Sign of the Turtox
Pledges Absolute Satisfaction

GENERAL BIOLOGICAL SUPPLY HOUSE
[Incorporated]
761–763 EAST 69TH PLACE
CHICAGO, ILL., U. S. A.

LEITZ
ULTROPAK ILLUMINATOR



Leitz Ultropak Illuminator attached to large Pillar Stand

SPECIAL FEATURES:

1—Illumination free from internal reflections.

2—Glare from moist or glossy surfaces can be eliminated through polarizing attachment.

3—Special Immersion Attachments permit observation of objects submerged in water or other liquids.

4—Special pillar stands make observations of large objects possible (stems, leaves, etc.)

WRITE FOR DESCRIPTIVE LITERATURE

E. LEITZ, Inc., Dept. 629

60 East 10th Street

New York City

BRANCHES:—Washington, D. C., Chicago, Ill., San Francisco, Calif., Los Angeles, Calif.